

Rhodora

JOURNAL OF THE
NEW ENGLAND BOTANICAL CLUB

Vol. 94

October 1992

No. 880

RHODORA, Vol. 94, No. 880, pp. 327-339, 1992

BV 004 105 /
ONTROPIS? newer
Syn. = dist.

CLIMATE AND THE DISJUNCT DISTRIBUTION OF *POLYSTICHUM ALFARII* (CHRIST) BARR., COMB. NOV. IN MESOAMERICA

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ABSTRACT

Polystichum alfarii (Christ) Barr. is here recognized as a species with a wide disjunction from the montane regions of northern Mesoamerica to the mountains of Costa Rica and Panama. Morphological circumscription and a meiotic chromosome number of $n = 41$ bivalents are provided. Comparison of habitat and distribution with other Central American species of *Polystichum* suggests that the 620 km disjunction of *P. alfarii*, noteworthy for a lower-altitude *Polystichum* species in Mesoamerica, is related to its unique preference for seasonally dry forests at altitudes between 1300 and 1700 m.

Key Words: *Polystichum alfarii*, plant nomenclature, disjunction, biogeography, climate and distribution, Mesoamerica

INTRODUCTION

Polystichum, though not the most diverse fern genus in Latin America, has presented unique problems in recognizing species boundaries. Many of these problems are biological: environmentally induced and developmental variation often obscures evolutionary relationships in the genus (Barrington, 1985). Species unrecognized for strictly historical reasons (taxonomic and nomenclatural) have also made it difficult to understand evolutionary relationships in the genus. In 1980, Alan Smith described a distinctive new species of *Polystichum* from Oaxaca, Mexico, which he named after John Mickel, co-author of the recent fern flora for that region (Mickel and Beitel, 1988). Smith excluded a

small set of materials that differed from *P. mickelii* A.R. Smith in having a true indusium (A. R. Smith, 1981: 200). Recognition of these materials as a distinct species of the Mexican endemic center, also including a large series of plants from southern Mesoamerica, is the subject of this contribution.

METHODS

The work reported here is based on a morphological analysis of a set of about 60 collections (often represented by one or more duplicates) from the following herbaria: BM, CR, DUKE, F, GH, IJ, MO, NY, UC, US, VT, and YU. Thanks are extended to these herbaria for providing loans of materials for this project. This work was carried out in the course of preparing a treatment of *Polystichum* for the Flora Mesoamericana. In the course of ongoing fieldwork in Costa Rica, I encountered the new species (*P. alfarii*) in two sites in the Valle Central; these sites have made additional work with living plants possible. I have not seen the plant in the field at any Mexican or Guatemalan sites.

In January 1991, I collected a sample of 23 living sporophytes from the Cerro Tablazo population, which served as the material for a report of basic information on chromosome number and behavior in meiosis I. Cytological technique largely followed Barrington, 1990.

RESULTS

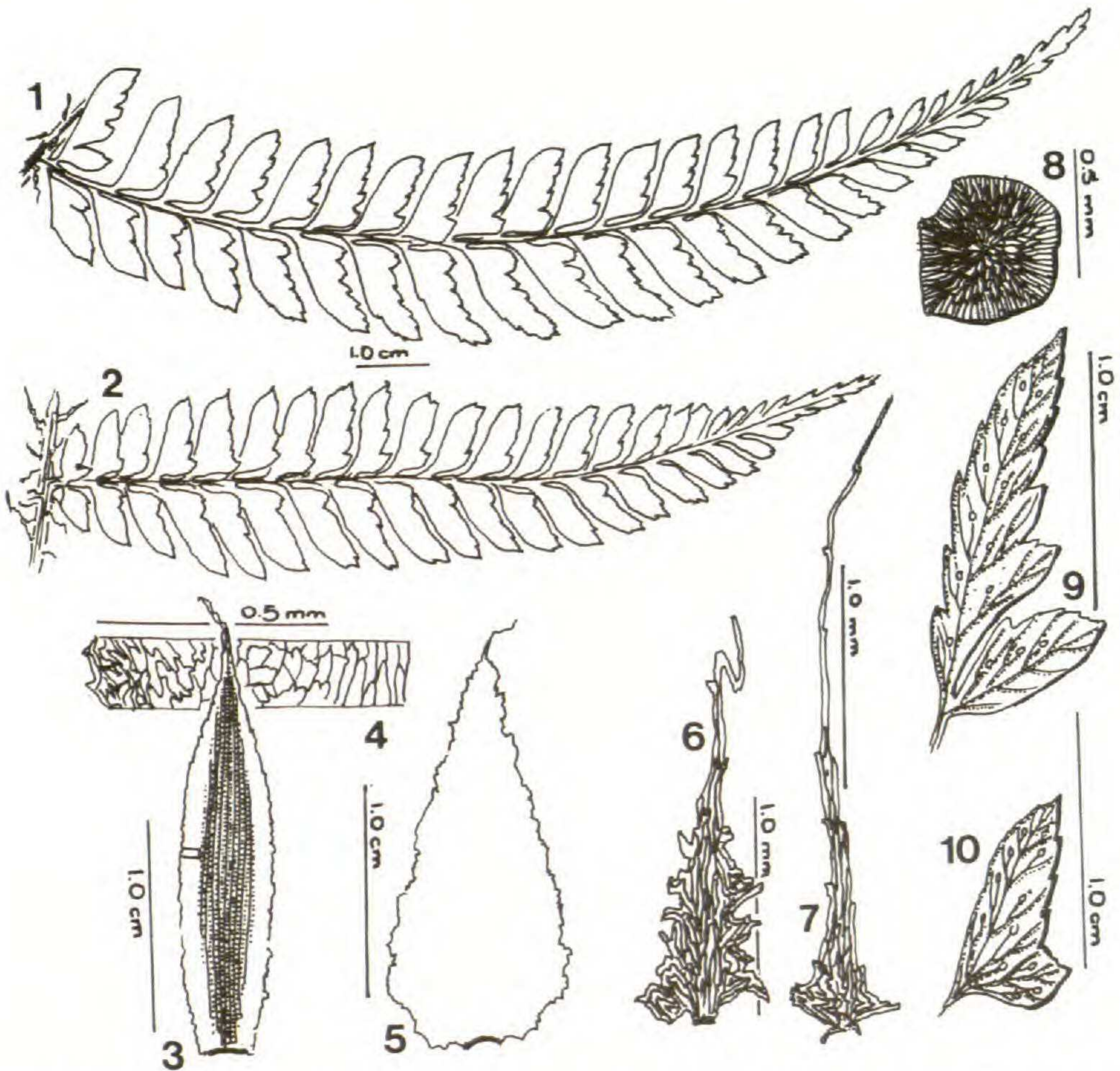
Systematic Section

Polystichum alfarii (Christ) Barr. *comb. nov.* (Figures 1–10)

Polystichum aculeatum (L.) Roth var. *alfarii* Christ, Bull. Herb. Boissier II. 4: 963 (1904). HOLOTYPE: Costa Rica, Alajuelito, 1300 m, March 1902, Alfaro 16471, P not seen; ISOTYPE: US!

Polystichum aculeatum (L.) Roth, var. *flavidum* Rosenstock, *Repert. Spec. Nov. Regni. Veg.* 22: 9 (1925). SYNTYPES: Costa Rica, Carthago, 1400 m, 16.IV.1910, Brade 555, UC!; Costa Rica, Carpintera, 10.IV.1908. Brade 26a, NY!

Rhizome 2–6 cm diam., unbranched; proximal petiole scales lanceolate, center coriaceous, dark reddish brown, border chartaceous, orange-yellow, marginate throughout, the margin irreg-



Figures 1–10. *Polystichum alfarii* (Christ) Barr. 1. Median pinna, *Barrington 1242* (VT). 2. Basal pinna, *Barrington 1242* (VT). 3. Basal petiole scale, *Steiermark 35194* (F). 4. Detail of edge of basal petiole scale near the center as indicated in Figure 3. 5. Distal petiole scale, *Steiermark 35194* (F). 6. Small scale from petiole, *Alfaro 137* (US). 7. Small scale from pinna-rachis, *Steiermark 35194* (US). 8. Flange of true indusium from above, *Alfaro 137* (US). 9. Larger, more dissected pinnule, *Steiermark 35194* (F). 10. Smaller, less dissected pinnule, *Jiménez 395* (CR).

ular, with a few short rigid to flaccid cilia throughout; distal petiole scales similar, but broad-lanceolate, uniformly papyraceous, orange-yellow or reddish orange with an orange-yellow border, conform or marginate except at base; small scales of petiole mostly ovate-caudate or long-lanceolate (less often deltate or broad-lanceolate), color various but generally dark, marginate at least at base; lamina 37–100+ cm, 2-pinnate-crenate to 2-pinnate-pinatifid, acuminate; rachis without a proliferous bud, rachis scales light yellowish brown; pinnae 10–16 × 2–2.5 cm, attached at more or less right angles to rachis; pinna-rachis scales filiform or

less often narrow-lanceolate, with a few basal cilia, rare elsewhere; pinnules mucronate, flat, the basal acroscopic pinnules longer than the next distal; veins free, spinules developed only at pinnule tip, weak; sorus round, terminal on vein; true indusium 0.5–0.7 mm diam., irregularly peltate with a margin of narrow, radiate cells and a medulla of regular, slightly elongate cells, most often brownish orange.

The name *Polystichum alfarii* (Christ) Barr. honors Anastasio Alfaro, Costa Rican naturalist and first director of the Museo Nacional de Costa Rica, who made many important collections in the productive “Golden Age” of work on the flora of Costa Rica (1885–10) (see Gómez P., 1977). Alfaro provided early insights into the character of the Costa Rican flora as well as a concise catalog of species (Alfaro, 1887). The type collection, made by Alfaro in March of 1902, is from Alajuelita—now a densely populated suburb just south of San José.

Both Christ and Rosenstock recognized elements of *Polystichum alfarii* from Costa Rica as varieties of *Polystichum aculeatum* (L.) Roth, in keeping with the then popular solution to the problem of recognizing clear species boundaries in the genus *Polystichum*. These varietal names were never consistently applied to *Polystichum alfarii*; the species has most often been left undetermined in herbaria. When collections of *P. alfarii* have been identified, they have been interpreted as any of several species with Mexican affinities, most often *P. ordinatum* (Kunze) Liebm. (a superficially similar species endemic to Mexico and Guatemala), but also as *P. muricatum* (L.) Fée (a remotely allied species occurring sporadically throughout northern Latin American and the Antilles).

A. R. Smith (1981: 200) first drew attention to materials of *P. alfarii* from Chiapas and Guatemala by setting them apart as unnamed collections, which he described as resembling *P. mickelii*. Mickel and Beitel (1988: 315) suggested that this same set of plants from Chiapas and Guatemala might pertain to *P. smithii* Mickel & Beitel, since the two share characters of the indusium and petiole scales. However, *P. smithii* differs from *P. alfarii* in being a much smaller fern with conform (not strongly marginate) petiole scales and fertile pinnules attached at right angles to the pinna-rachis. Judging only from the history of collecting (see Appendix), *P. alfarii* is rarer in the northern part of its range. At the

southern limit for the species, the Panama collections of *P. alfariei* have completely escaped recognition until now.

The key features of *Polystichum alfariei* that allow identification are its small (0.5–0.7 mm diam.) but clearly marginate indusium, its strongly marginate but not ovate-caudate or basally thickened petiole scales with dark reddish brown centers and orange-yellow borders, and its lustrous, mucronate pinnules attached obliquely to the pinna-rachis. Most prominent among features varying within the species is lamina dissection. The leaves vary from 2-pinnate crenulate to 2-pinnate pinnatisect, in contrast to most Mesoamerican species, in which leaf dissection of reproductive adults is relatively constant. The complex variation of this species and the superficially similar *P. mickelii* is best represented in a dichotomous key to the two taxa, especially because of the unusual petiole-scale variation in *Polystichum mickelii*.

KEY TO *POLYSTICHUM ALFARIEI* AND *P. MICKELII*

1. Proximal petiole scales strongly marginate, edge irregular, without superficial cilia, marginal cilia rare, not darkened; distal petiole scales strongly marginate, edge irregular, with a very few short, flaccid cilia; indusium present. 0.5–0.7 mm diam. *P. alfariei*
1. Proximal petiole scales conform or weakly marginate (margin narrow), edge regular, with or without superficial cilia, marginal cilia common, darkened or not; distal petiole scales conform (but isodiametric cells present apically), edge irregular, with many flaccid cilia, sometimes also with short, rigid, dark reddish brown cilia; indusium absent (forms of *P. mickelii*) 2
2. Proximal petiole scales without superficial cilia; marginal cilia common, dark reddish brown at least apically; petiole scurf with abundant cilia . . . *P. mickelii*, typical form
2. Proximal petiole scales with superficial cilia; marginal cilia rare or absent, pale orange-yellow; petiole scurf with few cilia *P. mickelii*, form with superficial cilia

Ecology

Unlike almost all *Polystichum* species in Mexico and Central America, this species is most common in moist forests, not wet

forests and rain forests (moisture adjectives are used in the quantitative sense of Holdridge, 1967); it has been reported from moist and dry forests and it persists in remnant forests. Among the few *Polystichum* species with a relatively low altitude preference, *P. alfarii* has been encountered between 1140 and 2200 m: about three-quarters of these collections are from between 1300 and 1700 m, with an overall mean altitude of 1540 m. Hence, this species is almost always found below the altitudes where cloud cover itself strongly influences climate (Troll, 1968). Only three out of the 22 species of *Polystichum* known from Mesoamerica (Barrington, 1993) occur at these lower altitudes. A typical *Polystichum*, *P. alfarii* shows a marked preference for the slopes above streambanks in steep terrain, perhaps indicative of a tendency for gametophytes to pioneer on the moister, unstable slopes near streams. The two study sites where I have seen this species in Costa Rica provide further insight into its ecology and hence its distribution.

At the Cerro Tablazo site above Tablón, in the central valley of Costa Rica (9°50'N, 84°01'W), a large population including plants in numerous size classes occupies an area of at least several hectares in the shade of an evergreen forest at 1600 m, near the median altitude for the species. There, plants are most frequent on very steep (40–60°) slopes in sight of and occasionally at the edge of the swift-moving Río Purires. Younger plants are especially frequent along vertical exposures of bare soil presumably persisting from past stream disturbances and slope wastage at the site. Older plants (often with leaves in excess of 1.5 m long) do not show the same preference for earthen exposures; presumably the disturbances they originally occupied have since been stabilized and obscured.

Climate at the Tablón site is markedly different from that typical of *Polystichum* sites in Costa Rica—Herrera (1985) maps the site as “clima subhumedo, caliente, con una estación seca moderada (35–70 días con déficit de agua).” The most frequent companion pteridophyte at the Cerro Tablón site is *Anemia phyllitides* (L.) Swartz, a species able to withstand considerable water stress. In contrast, typical Costa Rican sites for *Polystichum* species present much less demanding water-availability regimes. In addition, most sites provide less heat. Herbarium-sheet data suggest that *P. alfarii* is commonly found in regimes such as that encountered at Tablón.

By contrast, I have also seen *Polystichum alfarii* at Porrosatí

(10°06'N, 84°05'W), on the slopes of Volcán Barba, one of the series of volcanoes lying north of the central valley in Costa Rica. There, at the highest site at which the species has been encountered, the species is extremely rare—only one immature individual was seen in January, 1991. The Porrosatí site is a 5 m-deep ravine cut in recent volcanic sediments by the Río Ciruelas, which is surrounded by agricultural land cleared from cloud forest. The plants seen there all grew on the earthen walls of the ravine in deep shade. The poorer performance of this species at this higher, wetter site again suggests that, unlike other Costa Rican species, *P. alfarii* is a plant of drier, warmer forests. These forests, on the gentler lower slopes of the montane regions of the country and near the major population centers, are among those most disturbed by the human population.

Distribution

The most striking feature of *Polystichum alfarii*'s distribution is a range disjunction of 620 km, from the volcanic slopes above San Ramón in Costa Rica to Volcán de San Vicente in El Salvador (Figure 11). Similar disjunctions characterize the Central American distribution of three other *Polystichum* species (Table 1). The distributional hiatus defines two centers of distribution, one northern (Chiapas–El Salvador) and the other southern (Costa Rica–Panama). Also evident is a distribution unique for *Polystichum* along the Pacific (lee) slopes of the two montane regions. The single exception to the Pacific-slope rule is the set of now threatened central-valley populations in Costa Rica, where relatively dry moist-forest conditions are enforced in the lee of a volcanic range.

Cytology

Two plants from the Tablón population yielded counts of $n = 41$ bivalents at Meiosis I prophase (Figures 12, 13). These counts are based on four sporocytes for Barrington 1976 (VT) and two sporocytes for Barrington 1991 (VT).

Hybridization

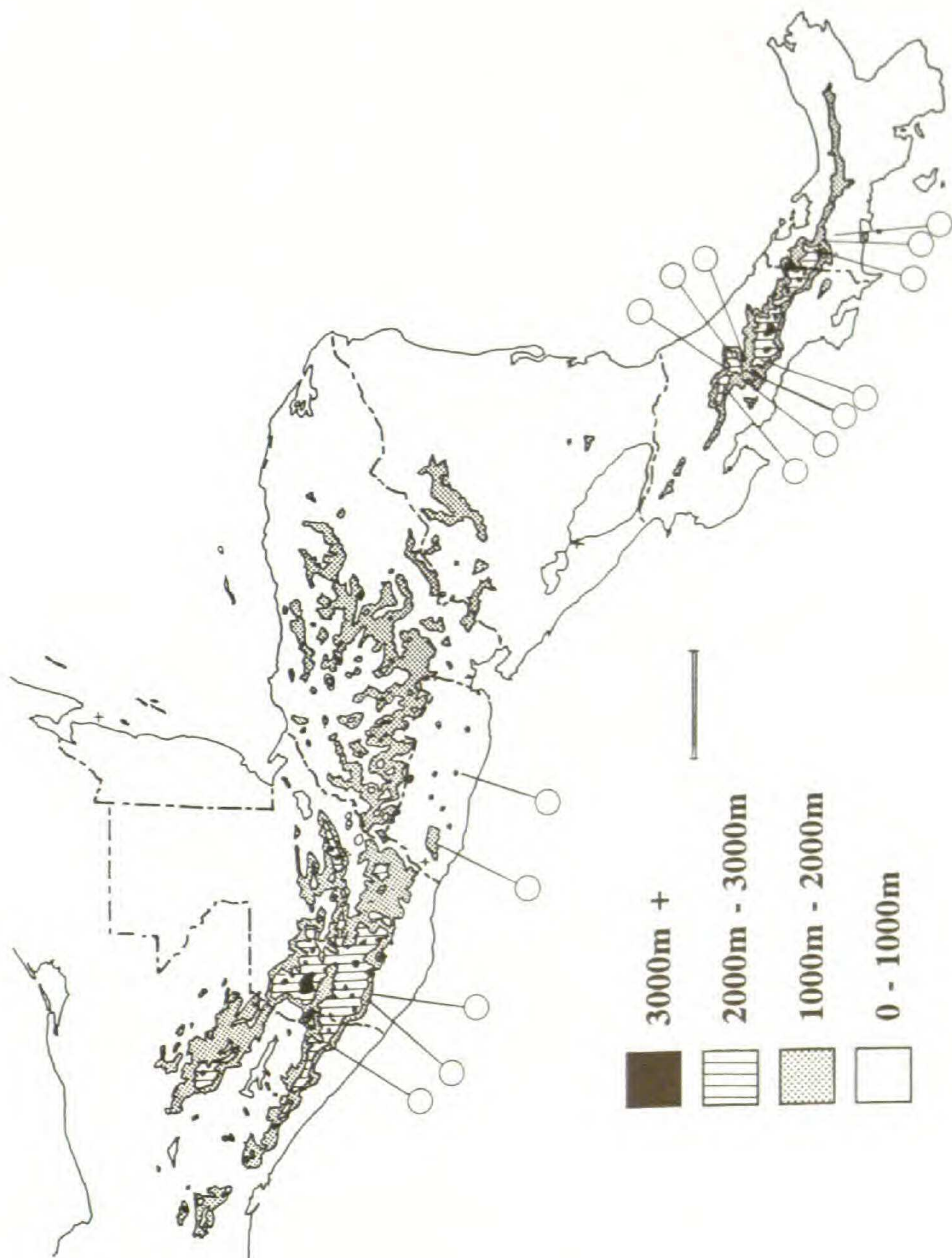
William R. Maxon has collected the hybrid between *Polystichum alfarii* and *P. platyphyllum* (Willd.) Presl, a widespread

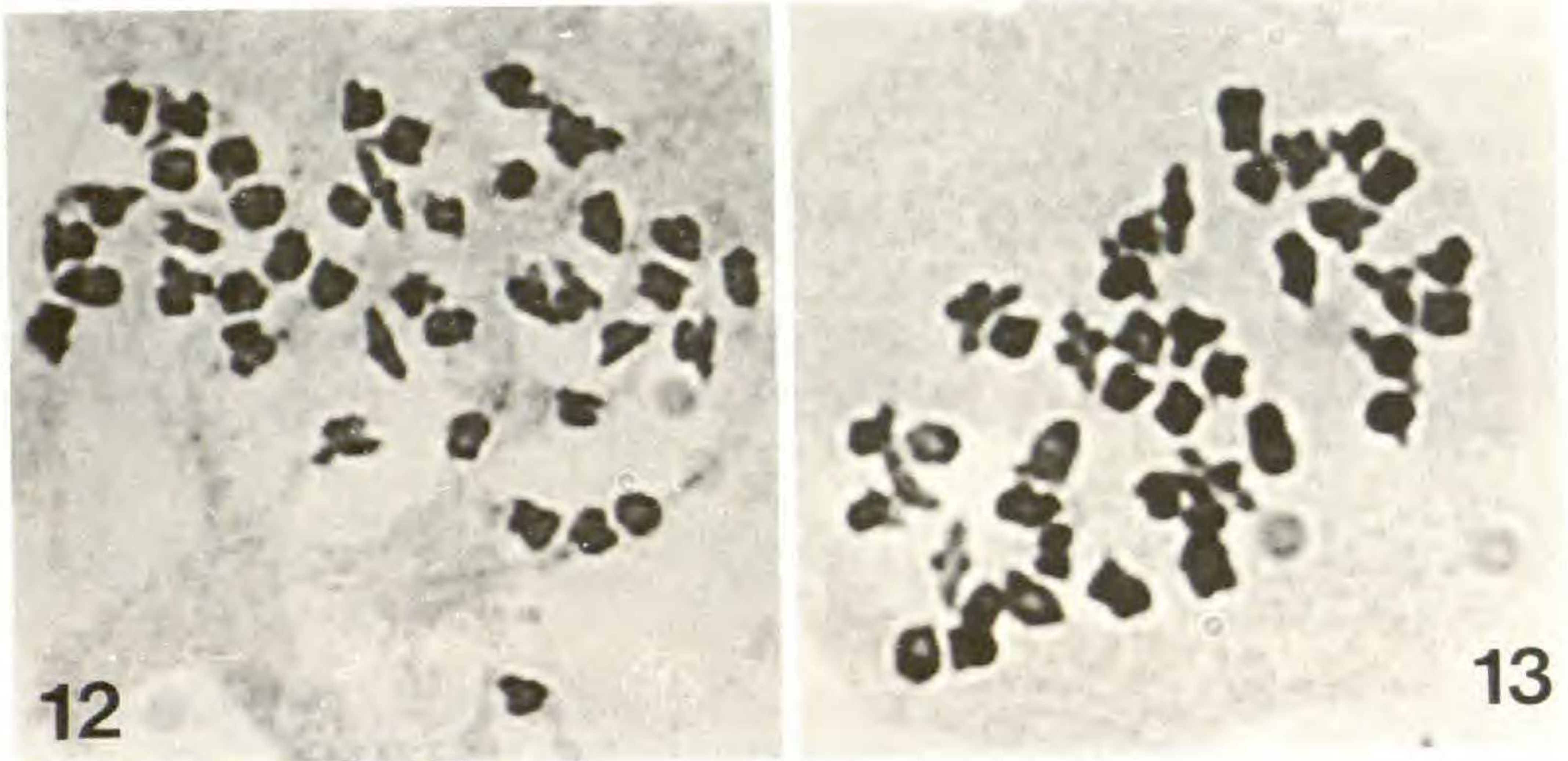
Table 1. Range disjunctions in the widespread Mesoamerican species of *Polystichum* (order is altitudinal range).

Species	Altitudes	Typical Habitat	Maximum Disjunction	Location of Disjunction (or Notes on Range)
<i>P. platyphyllum</i>	600–1500 m	Tropical & premontane wet forests	—	Missing from Guatemala and El Salvador
<i>P. alfarii</i>	1100–2200 m	Premontane moist forest	620 km	El Salvador - Costa Rica
<i>P. muricatum</i>	1100–2700 m	Lower montane wet forest	—	Missing only from El Salvador
<i>P. hartwegii</i>	1200–2700 m	Lower montane wet forest	—	Present throughout Mesoamerica
<i>P. fournieri</i> complex	1900–3100 m	Montane rain forest	550 km	Honduras - Costa Rica
<i>P. speciosissimum</i>	2600–3500 m	High-montane rain páramo	1010 km	Guatemala - Costa Rica
<i>P. orbiculatum</i>	3200–3600 m	High-montane rain páramo	1070 km	Mexico - Costa Rica

exindusiate species of lower-altitude wet and rain forests, from the east end of the Central Valley in Costa Rica. (Collection data: Costa Rica, Pr. Cartago, vicinity of Santiago, humid forest floor, 1050 m, April 20, 1906, *W. R. Maxon, 100, US 575664!*.) This hybrid combines the diagnostic subapical bud and attenuate apex of *P. platyphyllum* with the small indusium of *P. alfarii*. Sporangia of this hybrid rarely open and are largely collapsed. Altitudinally the hybrid is from near the median altitude for *P. platyphyllum* and just below the lowest altitude recorded for *P. alfarii* (Table 1).

Figure 11. Distribution of *Polystichum alfarii* (Christ) Barr. Contour intervals are 1000 m. Scale bar is 100 km. Only a few representative collections from the Valle Central of Costa Rica are plotted. Localities are at tip of line opposite the circle.





Figures 12 and 13. Meiotic chromosome number for *Polystichum alfarii* (Christ) Barr. Two cells in prophase of meiosis I, $n = 41$ pairs, D. S. Barrington 1976 (VT).

DISCUSSION

Comparison of the disjunct distributions of Central American *Polystichum* species (Table 1) reveals a relationship between altitude, rainfall regime, and the precise nature of the disjunction. The greatest disjunctions are characteristic of the species with the highest altitude preferences, e.g., *P. orbiculatum* (Remy) Fée and *P. speciosissimum* (Kunze) Tryon & Tryon; both species are confined to alpine or high-montane forest habitats that are limited in distribution in Mesoamerica. In contrast, two species with altitudinal ranges much like *P. alfarii*'s show no significant disjunctions because of the relative continuity of lower montane wet and rain forests where these species are common. *Polystichum alfarii* shows a disjunct distribution like that of evolutionary lineages such as the *P. fournieri* Smith species group from higher (cooler), more island-like montane habitats of Central America, presumably because of its adaptation to drier forests than the other species at equivalent altitudes.

Tryon (1972) portrayed fern species diversity in tropical America in the context of endemic centers. These centers evidence high total numbers of species and high percentages of endemic species; they are separated from others by regions poor in total species and endemic species. Several of his inquiries revealed patterns consistent with an origin of diversity via an evolutionary migration scheme, in which lineages reached different endemic centers

via long-distance dispersal and then diverged from source species in the new region (e.g., *Sphaeropteris*; Tryon, 1971). This scheme is the continental equivalent of inferred histories for insular endemics such as the genus *Diellia* in Hawaii (Wagner, 1952).

Understanding the process by which species diverge in tropical montane regions is dependent on the resolution of species and vicariant species pairs showing disjunct distributions between endemic centers; *Polystichum alfarii* is such a species. More generally, the genus *Polystichum* is of particular interest as a system for the study of the process of evolutionary migration because it is a montane group including a diversity of species with a variety of climatic preferences. The apparent relationship between this variety and geographic distribution suggests that the genus has the potential to provide insight into the determinants of successful diversification in endemic centers.

ACKNOWLEDGMENTS

The University of Vermont provided support for field work in Costa Rica through its Institutional Grant #BSCI90-8. Cathy Paris contributed valuable insights and a critical review. An anonymous reviewer added substantially to the quality of this work.

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APPENDIX

Exsiccatae for *Polystichum alfarii* (Christ) Barr.

- ✓MEXICO. ✓Chiapas: Finca Irlanda. C. A. Purpus 7231, 7232 (US), 7243 (GH, MO, US), 7243A (BM).
- ✓GUATEMALA. ✓Dept. Quetzaltenango: along Río Samalá, between Santa María de Jesús and Calahuaché, 1200-1300 m, J. A. Steyermark 33834 (F, US); slopes of Volcán Santa María, 1 mi. below Santa María de Jesús, 1520 m, J. A. Steyermark 34367 (F); Finca Pirineos, between Santa María de Jesús and Calahuaché, 1350 m, J. A. Steyermark 35194 (F).
- ✓EL SALVADOR. ✓Pr. Ahuachapán: Sierra de Apaneca, region of Finca Colima, P. C. Standley 20135 (GH, US). ✓Pr. San Vicente: Volcán San Vicente, 1450 m, W. Lötschert 84 (US); Volcán San Vicente, P. C. Standley 21489 (US).
- ✓COSTA RICA. ✓Pr. Alajuela: La Ventolera, S slope of Volcán Poás, 1700 m, P. C. Standley 34646 (US). ✓Pr. Cartago: Cartago, 1300 m, A. Alfaro s.n., dist. as J. Donnell Smith 6961 (US); just above Tablón on road up E side of Cerro Tablazo, 1600 m. 9°50'N × 84°01'W, D. S. Barrington 1242 (CR, VT), 1976, 1991 (VT); Carpintera, 1700 m, A. Brade & A. C. Brade 26 (GH); Malavassi coffee finca, S of Tres Ríos, 1200 m, F. M. Givens 3195 (F); in Lankester Garden, 4750' (native fern), E. Scamman 5925 (GH); Pacayas, foot of Volcán Turrialba, 1400 m, E. Scamman 7080 (US); above Tres Ríos, 5000', E. Scamman & L. R. Holdridge 7945 (US); Cerro de la Carpintera, 1500-1850 m, P. C. Standley 34227 (US); Dulce Nombre, 1400 m, P. C. Standley 35956 (US); La Carpintera, 1800 m, R. Torres R. 170 (US); Tablazo, 1877 m, M. Valerio on 8-1-27 (CR 33362); Hacienda Linda

Vista, just S of Dulce Nombre de Culmi, SE of Cartago, 1300 m, *E. J. Judziewicz* 4370 (CR, MO). **Pr. Herédia:** 1.7 km NNE of Porrosatí, on the Río Ciruelas, 2200 m, 10°06'N × 84°05'W, *D. S. Barrington* 1213 (CR, VT). **Pr. San José:** Río Herradura, tributary of the Río Chirripó del Pacífico, NW of Canaán, General Valley, 1600 m, 9°29'N × 83°37'W, *W. C. Burger & R. L. Liesner* 7084 (CR, F); Hacienda La Verbena, Río Tiribí, Alajuelita, 1140 m, *O. Jiménez L.* 395 (CR, US). Río Torres: San Francisco de Guadalupe, *O. Jiménez* 360 (CR), San Francisco de Guadalupe, 1150 m, *H. Pittier* 7153 (CR, US), 7155 (CR); Cerro de Piedra Blanca, above Escasú, *P. C. Standley* 32501, 32533 (US); San Francisco de Guadalupe, *A. Tonduz* 9837 dist. as *J. Donnell Smith* 7216 (GH, US); El Copey, Río Pedregoso, 1800 m, *A. Tonduz* 11853 *p.p.* (CR; the US collections of this number are *P. concinnum* Lellinger ex Barr.).

PANAMA. **Pr. Chiriquí:** vic. "New Switzerland," central valley of Río Chiriquí Viejo, 1800–2000 m, *P. H. Allen* 1334 (US); Guadalupe, Cerro Punta, 2000 m, *R. Caballero* 149 (MO); between Holcomb's trail and Mouniche plantation, above El Boquete, 1500–1725 m, *E. P. Killip* 5086 (US); Piedra de Lino, El Boquete, 1400–1600 m, *E. P. Killip* 5410 (US); N side of Río Caldera, Horqueta - Bajo Mano, NW of Boquete, *J. L. Luteyn* 4581 (DUKE); above Sabana de El Salto, trail to Camp Aguacatal, E slope of Volcán Chiriquí, 1500–1750 m, *W. R. Maxon* 5267 (US); km 10.7 on Volcán–Cerro Punta Rd., *G. R. Proctor* 32005 (U).